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REVISION OF HETEROTHECA, SECTION HETEROTHECA (COMPOSITAE)¹

BURDETTE L. WAGENKNECHT

Heterotheca until recently has been considered to be a small genus of the tribe Astereae and has not been treated systematically since De Candolle's revision for the *Prodromus* (1836). Shinnars (1951) merged *Chrysopsis* with *Heterotheca*, resulting in a considerably enlarged genus. Acceptance of this merger requires that the species constituting *Heterotheca sensu stricto* should be placed in *Heterotheca*, section *Heterotheca*, and the remaining species arranged in various sections similar to those in which they had been previously placed in *Chrysopsis*.

Heterotheca section *Heterotheca* is native to continental North America and is an occupant of sandy or disturbed habitats. It ranges from Long Island south to Georgia and Florida on the coastal plain, west to California and from Illinois southwest to the state of Oaxaca, Mexico. It has been introduced in Brazil and Hawaii and one species is rarely cultivated in Europe.

The present treatment is based upon the examination of

¹Part of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Kansas. I should like to take this opportunity to express my appreciation to Prof. R. L. McGregor for his advice and assistance while directing this study. The critical examination of the manuscript by Dr. L. H. Shinnars of Southern Methodist University has been helpful. A grant from the Society of the Sigma Xi made possible much of the field work undertaken in connection with this study.

more than 1500 specimens from fifteen² herbaria, and a study of three species and their varieties in the field. Only a limited number of representative specimens are cited for most of the taxa involved. A complete list of all specimens examined in this study may be found in the original thesis at the Library of the University of Kansas.

GENERIC RELATIONSHIPS

The first species of *Heterotheca* was described as a species of *Inula*. *Heterotheca* can be separated from *Inula* and the tribe Inuleae by the flattened and smooth style-branches, extended into lanceolate hairy appendages and by the obtuse and barely notched anther bases. Bentham and Hooker (1876) placed the genus *Heterotheca* in the tribe Astereae. The most closely related genus is *Chrysopsis*, which shows great similarity in its morphology and its preference for sandy habitats. *Heterotheca* as a genus is of a more weedy nature. These two genera are usually maintained as separate entities because of the absence of a pappus from the ray achenes in *Heterotheca* and the presence of a well-developed double pappus on the ray achenes in *Chrysopsis*.

At least two authors have felt that the two genera should not be separated. Baillon (1886) not only merged *Chrysopsis* and *Heterotheca* with *Hysterionica* but also included *Grindelia*, *Pentachaeta*, *Aphantochaeta*, *Bradburia*, *Happappus*, *Xanthisma*, *Chrysothamnus* and *Lessingia* under the same genus. The above listed genera were to be considered as sections of *Hysterionica*. No transfers of species were made. The elongated lanceolate stylar appendage can be used to separate *Heterotheca* and *Chrysopsis* from *Hysterionica*, which has a short deltoid stylar appendage.

Shinners (1951) questioned only the segregation of *Heterotheca* and *Chrysopsis* and pointed out that it seemed unreasonable to preserve all the diverse sections of *Chrysopsis* within the same genus and to exclude *Heterotheca*,

²The abbreviations employed in referring to these herbaria are those of Lanjouw and Stafleu (1952) and are as follows: CU, Cornell University; F, Chicago Natural History Museum; GH, Gray Herbarium; KANU, University of Kansas; MEXU, Universidad Nacional de Mexico; MO, Missouri Botanical Garden; NEB, University of Nebraska; NY, New York Botanical Garden; OKLA, Oklahoma State University; P, Museum National d'Histoire Naturelle; PH, Academy of Natural Sciences of Philadelphia; SMU Southern Methodist University; TEX, University of Texas; UC, University of California; and US, United States National Herbarium.

which resembles closely certain sections of *Chrysopsis*. In particular he thought it inconsistent to segregate *Heterotheca* based on the absence of the pappus from the ray achenes and to maintain the section *Ammodia*, as a part of *Chrysopsis*, even though the entire ray cycle of the head was missing.

One line of investigation which offered the best interpretation of this situation was a study of the pappus characters of all specimens studied. In all manuals treating the genus, there are references to the presence of at least a rudimentary pappus on the ray achenes. De Candolle considered *Heterotheca chrysopsidis* to be sectionally distinct from the remainder of the genus because of the presence of a pappus on the ray achenes. His use of the epithet *chrysopsidis* is a reflection on his observation of an intermediate character between *Heterotheca* and *Chrysopsis*. Examination of the isotypes of this species reveals that the pappus characters indicated by De Candolle were not consistent in all specimens within the type collection.

Studies of all collections throughout the genus revealed that approximately three per cent of the specimens examined bore a rudimentary pappus. One specimen, *F. B. Jones 430*, from San Patricio Co., Texas (OKLA), is of great interest. The ray achenes produced by this plant bear a double pappus indistinguishable from that of the disk achenes. In addition to the presence of a pappus, the ray achenes further resemble the disk achenes in that they are densely sericeous. Another specimen (SMU), bearing an identical label and of identical appearance, has glabrous, epappose ray achenes. Any attempt to identify these two plants with current keys other than those of Shinnars (1958) would result in the placing of these two specimens in different genera. The discovery of such wide variability of the pappus within *Heterotheca*, including that characteristic of *Chrysopsis*, leads me to support Shinnars' conclusion that the two genera should be merged.

One other genus shows some relationship with the group studied. *Croptilon* (*Isopappus*; often included in *Haplopappus*) can be distinguished from *Heterotheca* by the single pappus found on the disk achenes. Those specimens of *Heterotheca grandiflora* in which disk achenes lack an outer

pappus show a trend in this direction. However, the merging of *Croptilon* with *Heterotheca* could not be recommended without a great deal of further study.

Chromosome numbers have not provided any evidence for or against the merger of these genera. Darlington's lists (1956) show $n=9$ to be the most common number in the tribe Astereae. This was the number found in *Heterotheca grandiflora* by Heiser (1948). Dr. R. C. Jackson, Department of Botany, University of Kansas, and I found $n=9$ in *H. latifolia* var *macgregoris*. (Voucher specimen *Wagenknecht 4640*, 1 mi. s. Coldwater, Comanche Co., Kansas, on file at the Herbarium of the University of Kansas (KANU)). Dr. B. L. Turner, University of Texas, informs me in private correspondence that he has unpublished counts $n=9$ in *Chrysopsis graminifolia* and *Heterotheca inuloides*. Dr. R. C. Jackson (1959) has a count of $n=18$ in *Chrysopsis foliosa* Nutt. Dr. Turner (1959) has reported $n=5$ in *Chrysopsis pilosa* and more recently, he sent me a manuscript by Mr. M. O. Cherry, Biology Department, Pasadena High School, Pasadena, Texas, correcting this latter number to $n=4$.

TAXONOMIC TREATMENT

Heterotheca Cassini, Bull. Soc. Philom. 137. 1817

Calycium Ell., Sketch 2: 338. 1824.

Diplocoma D. Don in Sweet, Brit. Fl. Gard. 3: 246. 1828.

Stelmanis Raf., Fl. Tellur. 2: 47. 1836.

Heterotheca section *Chaetactis* DC., Prod. 5: 317. 1836.

Heterotheca section *Gymnactis* DC., Prod. 5: 317. 1836.

Hysterionica section *Heterotheca* Baillon, Histoire des Plantes 8: 155. 1886.

Annual, biennial, or perennial, simple, or branched aromatic herbs. Stem strict, ascending, or decumbent, striate, pilose, sericeous, scabrous or glandular-hairy. Leaves alternate, simple, entire, dentate to serrate, ovate to lanceolate, to elliptical, scabrous to hirsute above, scabrous to pilose below. Basal and lower cauline leaves petiolate, the petioles often with auriculate-clasping bases; upper cauline leaves sessile. Inflorescence paniculate to corymbose, the heads on short lateral branches, smaller than those terminating main branches. Heads hemispheric to broadly campanulate, the phyllaries in 4-6 series, glabrous, glandular-hairy, scabrous or sericeous, the inner series with scarious edges, the tips pilose. Ray flowers numerous, pistillate, often abortive, spreading, characteristically rolling into a tight coil when dried, narrowly ligulate, or linear, each terminated by three teeth, tubular at the base,

the tube pubescent, producing a slender glabrous style, and a narrow, glabrous, bifid stigma, the achene trigonous, glabrous to slightly sericeous, the pappus absent or present as a toothed crown or as a few caducous bristles. Disk flowers numerous, perfect, tubular, slender at the base and widening upwards, five-toothed, five-nerved, the nerves alternate with the ovate-lanceolate, acute, spreading teeth. Stamens five, naked at the base with deltoid appendages at the apex, exerted from corolla at anthesis. Style glabrous, bifid, short, villous at the acute apex. Achene compressed, hispid to sericeous, crowned with a radiately spreading double pappus, the inner series of long, brown, slender, barbellate hairs, the outer series of short, flat, chaff-like appendages or of short, barbellate hairs, white or of the same color as the inner series. Receptacle flat, alveolate, the partitions between the achenes scarious, the points very unequal.

Native to the United States and Mexico, introduced in Hawaii and Brazil. TYPE SPECIES: *Heterotheca subaxillaris* (Lam.) Britton & Rusby.

In 1824, Elliott proposed a provisional genus *Calycium*, depending upon whether *Inula scabra* Pursh should be considered sufficiently distinct to warrant generic segregation. However, no transfer of the specific epithet was made.

KEY TO SPECIES AND VARIETIES

1. Habit strict, — 1-2.5 m. tall (spring form 10-30 cm. tall); stem 0.9-1.7 cm. in diameter; cauline leaves petiolate below, sessile above, coarsely serrate to entire; inflorescence of short, paniculate axillary branches; peduncles and phyllaries densely capitate-glandular.
..... *H. grandiflora*.
1. Habit erect to procumbent, if strict; inflorescence corymbose; stems less than 0.9 cm. in diameter, or if larger, with cordate, clasping, cauline leaves; peduncles and phyllaries not densely capitate-glandular.
 2. Habit erect or of several strict stems from a central caudex; lateral branches not well developed; inflorescence corymbose; leaves lanceolate; peduncles elongate and devoid of leaves.
 3. Perennial, several strict stems arising from a central caudex; heads 1.5-3.0 cm. in diameter, broadly campanulate.
 4. Stem and leaves densely pilose to villous; phyllaries densely villous with large jointed hairs. *H. inuloides* var. *inuloides*.
 4. Stem and leaves pilose; phyllaries with sparse, slender hairs.
..... *H. inuloides* var. *rosei*.
 3. Annual, heads 0.5-1.2 cm. in diameter, narrowly campanulate.
..... *H. leptoglossa*.
 2. Habit erect to decumbent, the lateral branches well developed; leaves ovate, elliptical to lanceolate; inflorescence paniculate to paniculate-corymbose; peduncles remotely to densely foliar.
 5. Perennial from well-developed woody caudex; blades of basal and cauline leaves ovate to elliptical, serrate to rarely entire, petiolate, the petioles of basal leaves up to 4 cm. in length; pappus a deep reddish-brown. *H. chrysopsidis*.

5. Annual or weakly perennial, the caudex not developed; leaves elliptical or lanceolate, serrate to entire, the petioles of basal leaves less than 3 cm. long; pappus tan to white.
6. Habit erect to decumbent, up to 1 m. tall, the stem scabrous; lower leaf surface scabrous; phyllaries with well-defined tuft of short thick hairs on outer surface.
7. Habit erect; basal leaves serrate, the lateral veins readily discernible. *H. subaxillaris* var. *subaxillaris*.
7. Habit procumbent; basal leaves entire or remotely serrate, the veins obscure. *H. subaxillaris* var. *procumbens*.
6. Habit erect, up to 2 m. in height; stem and lower leaf surfaces velutinous or pilose, the upper leaf surface scabrous to pilose; phyllaries sericeous and sparsely glandular.
8. Stem up to 1.2 cm. in diameter, the lateral branches coarse; leaves cordate-clasping, sparsely pilose above; phyllaries densely glandular and pilose. *H. psammophila*.
8. Stem 4-9 mm. in diameter, the lateral branches slender, or if coarse, leaves long-pilose; phyllaries not densely glandular.
9. Leaves scabrous above; heads less than 0.9 cm. in width. *H. latifolia* var. *latifolia*.
9. Leaves pilose or velutinous above; heads more than 0.9 cm. wide.
10. Lateral branches slender; leaves oblong-lanceolate, the veins not prominently raised. *H. latifolia* var. *macgregoris*.
10. Lateral branches coarse; leaves elliptical to lanceolate, the veins prominently raised. *H. latifolia* var. *arkansana*.

1. ***H. grandiflora*** Nutt., Trans. Am. Philos. Soc. Ser. 2, 7: 315. 1841
Diplopappus scaber (Pursh) Hook., Fl. Bor. Am. 2: 22. 1834.
 Not *Heterotheca scabra* (Nutt.) DC.; *Inula scabra* Nutt.; *Inula scabra* Pursh. *Heterotheca floribunda* Benth in Hinds, Bot. Sulph. 24. 1844.

Annual or biennial, somewhat rosulate, aromatic herbs, 0.5-2.5 m. (spring form 10-30 cm.) tall, unbranched below or with serotinous, assurgent basal branches. Stem striate, coarse, up to 1.7 cm. in diameter at the base, glandular-hairy above, progressively more densely hirsute below with spreading hairs up to 6 mm. long. Leaves ovate to elliptical or oblong, serrate to entire, 5-8 cm. long, 2-3 cm. wide, pilose on both surfaces. Lower cauline leaves petiolate, the petioles 3-7 cm. long, expanded into auriculate-clasping bases. Cauline leaves progressively smaller upwards, 2-4 cm. long, 0.5-1.5 cm. wide, sessile, coarsely serrate, oblong-lanceolate. Inflorescence paniculate-axillary, the involucres at the tips of the terminal branches 9-14 mm. wide, 6-9 mm. high, those of the short lateral branches 9-14 mm. wide, 6-9 mm. high, the heads campanulate to hemispherical. Phyllaries in 4-6 series, the outer series 3-5 mm. long, the inner series 6-9 mm. long, densely

capitate-glandular on the outer surface, the margins scarious, the apex villous. Ray flowers 25-40, the corolla-tube 4-7 mm. long, the ligule 5-8 mm. long; disk flowers 30-75, the tube 4-6 mm. long. Ray achenes 2-5 mm. long, epappose, trigonous, glabrous or slightly sericeous on the angles. Disk achenes 4-6 mm. long, obovate, compressed, sericous. Pappus of two series, the inner series of numerous barbellate bristles, 6-9 mm. long, reddish brown to white, the outer series squamellate setaceous or of short barbellate bristles 0.4-0.7 mm. long, or absent. Receptacle flat, white, alveolate, the partitions irregularly terminated by unequal chartaceous teeth.

TIME OF FLOWERING: April to December.

TYPE AND TYPE LOCALITY: "Rocks, circa Santa Barbara." Nuttall. not seen.

DISTRIBUTION AND HABITATS: native in eastern Arizona, California, Sonora and Baja California, Mexico and introduced in Hawaii. Sandy or disturbed soils at altitudes from sea level to 2,000 feet.

The first reference to this species is that of Hooker (1834). He erroneously considered it to be *Inula scabra* Pursh and in his treatment of the species transferred it to the genus *Diplopappus* as *D. scaber*. The description of Pursh cites *Inula subaxillaris* Lam. as a synonym and is therefore illegitimate under Article 60 of the Rules of Nomenclature. Hooker's transfer of this illegitimate epithet is also illegitimate.

Heterotheca floribunda Benthham was collected in the vicinity of San Pedro and of San Quentin, California, areas in which *H. grandiflora* was at the time the sole representative of this genus. Benthham's description matches Nuttall's earlier description in all essential points and is here, as in most previous works covering this species, considered to be a synonym of *H. grandiflora* Nutt.

The weedy nature of the species is shown by the appearance on a great many labels of habitats described as disturbed ground, fields, lots and roadsides. The creation of these habitats through urbanization and agricultural practices has increased its range. An indication that it is extending the northern boundaries of its range can be shown by a study of the dates of earliest collections in various California counties. In general, the first collections in counties south of San Francisco bear dates at least twenty-five years earlier than those of counties north of San Francisco.

Degener (1934) states that this species was introduced into the Hawaiian Islands before 1920. St. John and Hosaka

(1932) reported *Heterotheca grandiflora* as a noxious weed of the pineapple fields of Hawaii.

Representative specimens. **Arizona:** Santa Rita Forest Reserve, *Griffiths 5977* (US). **California:** Alameda Co.: *Rose 49180* (NY). Butte Co.: 1 mi. above Pentz, *Heller 15840* (UC). Contra Costa Co.: Antioch, *E. Crum 1731* (UC). Fresno Co.: *Brandeggee, July 20, 1905* (US). Los Angeles Co.: bank of Arroyo Seco, *Grinnell 377* (F); Catalina Island, *Nuttall 864* (F). Monterey Co.: 1 mi. northeast of Elkhorn, *Axelrod 616* (UC). Orange Co.: *Mason 2901* (UC). Placer Co.: Wheatland, *Heller 13833* (F, US). Riverside Co.: Riverside, *Barrus 22* (CU). San Benito Co.: *Balls 15890* (OKLA). San Bernardino Co.: San Bernardino Valley, *S. & W. Parrish 177* (F, GH, NY, P, PH, UC, US). San Mateo Co.: *Rose 34478* (OKLA). Santa Barbara Co.: near type area, Santa Barbara, *Eastwood 127* (F, GH, NY, UC, US). Santa Clara Co.: San Jose, *Davy 243* (UC). Santa Cruz Co.: 5 mi. S. Santa Cruz, *Wiegand 2416* (CU). Sonoma Co.: Northwood, *Hoffman* (UC). Stanislaus Co.: Oakdale, *Crum 1552* (UC). Tuolumne Co.: 1 mi. W. Confidence, *Belshaw 191* (UC). **MEXICO:** **Baja California:** 27 mi. N. Ensenada, *Wiggins and Gillespie 3969* (F, GH, MEXU, MO, NY, US). **Sonora:** *Fr. Thomas* (P).

2. *H. inuloides* Cass., Dict. Sci. Nat. 51: 460. 1827

Annual, biennial, or short lived perennial aromatic herbs, 50-150 cm. tall, unbranched below (second year's growth of several basal, assurgent branches arising from a central caudex), the stem striate, coarse, villous, green or various shades of purple. Leaves ovate to lanceolate, entire to serrate, 3-7 cm. long, 1-3 cm. wide, pilose on upper and lower surfaces. Lower cauline leaves petiolate, the petioles 2-8 cm. long, often with auriculate-clasping bases. Cauline leaves becoming progressively smaller above, 2-5 cm. long, 0.3-2 cm. wide, sessile, entire, lanceolate. Inflorescence corymbose. Involucres 1.5-3.0 cm. wide, 1.0-1.8 cm. high, hemispheric to broadly campanulate. Phyllaries in 4-6 series, the outer 2-4 mm. long, the inner 7-14 mm. long, densely villous to pilose on outer surface, the hairs prominently multicellular to unicellular, the tips purple, pilose, edges scarious. Ray flowers 25-40, the corolla tube 4-7 mm. long, the ligule 8-15 mm. long; disk flowers 40-60, the corolla tube 4-7 mm. long. Ray achenes 2-4 mm. long, trigonous, glabrous or with a few sericeous hairs. Disk achenes 2.5-5 mm. long, compressed, obovate, densely sericeous. Inner pappus of numerous barbellate bristles 4-9 mm. long, the outer squamellate-setaceous, or of short barbellate bristles 0.3-0.6 mm. long. Receptacle flat, white, alveolate, the partitions irregularly terminated by unequal chartaceous or occasionally fleshy points.

2a. *H. inuloides* var. *inuloides*

Diplocoma villosa D. Don, in Sweet, Brit. Fl. Gard. 3:246. 1828.

Doronicum mexicanum Cerv., in Link & Otto, Icones Pl. Rar. 43. 1828.

Leaves and stems densely pilose, the phyllaries densely villous with long jointed hairs.

TIME OF FLOWERING: April to December.

TYPE AND TYPE LOCALITY: Desfontaines, reported to be in the Herbarium Universitatis Florentinae, Florence, Italy. Cultivated in The Garden of the King. Grown from seeds thought to have come from DeCandolle, who thought they were of Mexican origin. Not seen.

DISTRIBUTION AND HABITATS: San Luis Potosi to southern Oaxaca, and from Orizaba to the western border of the state of Mexico. Sandy or sandy clay soils, open pine forests, fields, and roadsides, at altitudes of 4,000 to 10,000 feet.

Although Cassini (1827) was not sure of the country of origin or the manner in which the plant arrived at the Jardin du Roi, the description is quite precise. His description of the involucre and foliage permits no doubt that his plants belong to the variety *inuloides*.

Diplocoma villosa Don and *Doronicum mexicanum* Cerv. are not only well described but are also illustrated in detail. A comparison of these descriptions and illustrations with Cassini's description and with specimens of *Heterotheca inuloides* leaves no doubt that these are the same species.

This species has been used by the natives of central Mexico as a medicinal herb. The leaves and involucre are dried, packaged and sold in small shops under the common name "Arnica." The medicinal properties attributed to concoctions from this plant are similar to those attributed to the European Arnica and probably account for the common name. The illustration in Ramirez' (1898) account of the medicinal properties of the species appears to be of this variety, although there is no reason to expect that the following variety is not used for the same purpose.

Representative specimens. MEXICO: Federal District: Ajusco, *Lyonnet* 434 (GH, NY). Rio Frio, *Wagenknecht* 2783 (KANU); Temascaltepec, *Hinton* 847 (NY, SMU, US). Hidalgo: Valley of Tula, *Pringle* (PH, UC, US). Morelos: Cuernavaca, *Kenoyer* A 151 (F, GH). Oaxaca: Vincente Guerrero, *Wagenknecht* 2795 (KANU); Monte Alban, *Kenoyer* 1524 (GH). Puebla: Esperanza, *Pittier* 401 (US); Teziutlan, *Wagenknecht* 2825 (KANU). San Luis Potosi: San Luis Potosi, *Parry & Palmer* 372 (GH, NY, US). Vera Cruz: Orizaba, *Seaton* 164 (F, GH, NY, MO, US).

2b. *H. inuloides* var. *rosei* var. nov.

A varietate *inuloides* differt caule et foliis plus minusve pilosis, foliis ciliatis, phyllariis villosis.

Leaves and stem sparsely pilose, leaf margins ciliate, phyllaries sparingly villous.

The varietal epithet honors J. N. Rose whose comments on variation in this species led to the discovery of this variety.

TIME OF FLOWERING: April to December.

TYPE: *B. L. Wagenknecht 2846*, sandy soil along roadsides, 30 miles east of Guadalajara, Jalisco, Mexico. July 25, 1956. (KANU).

DISTRIBUTION AND HABITATS: States of Aguascalientes, Colima, Jalisco, Michoacán, Nayarit, and Zacatecas. Sandy soil along roadsides, in fields and open pine forests at altitudes of 3,000 to 5,000 feet.

This entity has been the source of some previous discussion. Gray (1887) examined *Palmer 268* from Guadalajara, Jalisco, and referred it to *Heterotheca leptoglossa* DC., regarding it as only a form of *H. lamarckii* Cass. [*H. subaxillaris*]. J. N. Rose (1894) examined the same specimen, noted the larger heads and more numerous rays, and placed it in *H. inuloides* Cass. as a form. My examination of this specimen has led me to agree more closely with Rose. The variation described above includes this specimen and is geographically distributed in a manner to warrant its treatment as a variety.

Representative specimens. MEXICO: **Aguascalientes:** Aguascalientes, *Hartweg 109* (NY). **Colima:** Tonila, *Jones 268* (US). **Jalisco:** Guadalajara, *Runyon 1352* (US), *Palmer 268* (US), Mazamitla, *McVaugh 13078* (SMU), 3 mi. S. Mazamitla, *Wagenknecht 2842* (KANU). **Michoacán:** Hidalgo, *Hitchcock and Stanford 7186* (NY, UC, US), Tancitaro, *Hinton 15477* (GH, PH). **Nayarit:** Tepic, *Palmer 2020* (US). **Zacatecas:** Suchil, *Gentry 8557* (GH, UC).

3. *H. leptoglossa* DC., Prod. 5: 317. 1836

Annual aromatic herbs, 0.5-1 m. tall. Stems strict, striate, hispid to pilose, the hairs up to 2.5 mm. long. Leaves lanceolate to linear-lanceolate, entire to dentate to serrate, 1.5-8 cm. long, 0.2-3 cm. wide, pilose on upper and lower surfaces. Cauline leaves progressively smaller upwards, 1-5 cm. long, 0.3-2 cm. wide, becoming sessile, entire. Lower cauline leaves serrate, petiolate, the petioles 1-2 cm. long, expanded into auriculate, clasping bases. Inflorescence corymbose, the heads borne at the tips of elongate leafless peduncles, the peduncles 4-10 cm. long, the heads narrowly campanulate 0.5-1.2 cm. in diameter. Phyllaries closely imbricated in 4-6 series, the outer series 2.5 mm. long, 0.5-0.8 mm. wide, glabrous to sparsely pilose. Ray flowers 15-30, the corolla tube 3-6 mm. long, the ligules 4-6 mm. long; disk flowers 25-40, the tube 4-8 mm. long. Ray achenes epappose, 2.2-3.8 mm. long, trigonous, glabrous or with a few sericeous hairs on the angles. Disk achenes 2.4-4.2 mm. long, ovate, compressed, densely sericeous. Inner pappus of numerous barbellate bristles 3.4-5.6 mm. long, the outer squamellate-setaceous, or of short barbellate bristles 0.3-0.5 mm. long.

Receptacle flat, white, alveolate, the partitions terminated by unequal chartaceous points.

TIME OF FLOWERING: February to December.

TYPE AND TYPE LOCALITY: *Mendez*, Guanajuato, Guanajuato, Mexico. Isotype (GH). Holotype Genève: Conservatoire et Jardin Botaniques (G). Not seen.

DISTRIBUTION AND HABITATS: Aguascalientes, Chihuahua, Guanajuato, Sinaloa, and Sonora, Mexico. Sandy soil, milpas, waste places and roadsides.

Heterotheca leptoglossa is an infrequently collected species. It has been confused with *H. latifolia* but is differentiated from the latter by its narrowly lanceolate leaves and corymbiform inflorescence. It is most closely related to *H. inuloides*, from which it is distinguished by its annual habit, narrow leaves, smaller capitulae, and linear phyllaries.

Representative specimens. MEXICO: Aguascalientes: Pesa Calles, *Shreve 9279* (GH). Chihuahua: Guicorichi, Rio Mayo, *Gentry 1947* (F, GH, MO, NY, PH, US). Guanajuato: San Miguel Allende, *Kenoyer 2178* (NY). Sinaloa: Choix, *Goldman 252* (GH, NY). Sonora: Alamos, *Goldman 289* (GH, US).

4. *H. chrysopsidis* DC., Prod. 5: 317. 1836

Perennial aromatic herbs, 25-75 cm. tall, branching from a woody caudex 2.5 cm. in diameter. Stem striate, slender, hispid to pilose, the hairs up to 2.5 mm. in length. Leaves ovate to elliptical, entire to serrate, 0.8-4 cm. long, 0.6-3 cm. wide, pilose on upper and lower surfaces, the veins prominently raised. Lower and middle cauline leaves petiolate, the petioles 1.5-4 cm. long, expanded into auriculate clasping bases. Cauline leaves becoming progressively smaller upwards, 0.4-2 cm. long, 0.2-1 cm. wide, sessile, serrate to entire. Inflorescence paniculately corymbose, the heads borne at tips of long flowering branches, the involucre 1-2 cm. wide, 0.5-1.2 cm. high, the involucre hemispheric to broadly campanulate. Phyllaries in 4-6 series, the outer series 2-3 mm. long, the inner series 6-9 mm. long, sparingly pilose. Ray flowers 15-30, the corolla tube 4-5 mm. long, the ligules 3-8 mm. long; disk flowers 30-50, the tube 4-7 mm. long. Ray achenes 1.5-2.5 mm. long, epappose or with a few setaceous bristles, trigonous, glabrous or with a few sericeous hairs on the angles. Disk achenes 2.5-4.0 mm. long, ovate, compressed, densely sericeous. Inner pappus of numerous barbellate bristles 6-9 mm. long, the outer series squamellate-setaceous, or of short barbellate bristles 0.2-0.4 mm. long. Receptacle flat, white, alveolate, the partitions terminated by unequal chartaceous points.

TIME OF FLOWERING: February to December.

TYPE AND TYPE LOCALITY: *Berlandier 109* "Circa Saltillo, " Mexico. Isotypes (F, GH, NY, PH); photographs of holotype (F, US). Holotype, Genève; Conservatoire et Jardin Botaniques (G). Not seen.

DISTRIBUTION AND HABITATS: Saltillo east to southern Nuevo León, Mexico. Sandy soils, fields, and roadsides, 1,000 to 3,000 feet.

De Candolle's (1836) description of *H. chrysopsidis* states that the ray achenes bear pappi. This characteristic led him to consider the species to be intermediate between *Heterotheca* and *Chrysopsis*. He described *Heterotheca* Section 1, *Chaetactis*, containing only this species. An examination of isotypes (F, GH, NY, PH) show that the character was not present throughout the type collection. In specimens of *H. chrysopsidis*, as in most other species, one finds a crown or a few caducous bristles present on the ray achenes. The characteristic is not distinctive enough to be used as a species character, or as a sectional character.

Representative specimens. MEXICO: Coahuila: Parra, *Johnston* 7707 (GH); Saltillo, *Palmer* 492 (GH, NY, PH, US). Nuevo León: Galeana, *Chase* 7670 (F, GH, MO, NY); 6 mi. below Iturbide, *Shreve and Tinkham* 9788 (GH); Monterrey, *Palmer* 481 (GH). Tamaulipas: San Jose, *Bartlett* 10277 (GH, US).

5. *H. subaxillaris* (Lam.) Britton & Rusby, Trans. N. Y. Acad.

Sci. 7: 10. 1887

Annual or biennial aromatic herbs, procumbent to one m. tall. Stem striate, slender, scabrous to strigose to hispid, the hairs up to 2 mm. long. Leaves ovate to elliptical or lanceolate, entire to dentate to serrate, 1-5 cm. long, 0.4-1.5 cm. wide, scabrous on both surfaces. Cauline leaves 0.3-1.8 cm. wide, 1-2.5 cm. long, becoming progressively smaller upward, sessile, serrate to entire. Lower cauline leaves petiolate, the petioles 1-2 cm. long with enlarged auriculate-clasping bases often present. Inflorescence a loosely spreading or divaricate corymbose panicle; terminal involucres 0.6-1.5 cm. wide, 4-8 mm. high, campanulate to hemispherical. Phyllaries in 4-6 series, the tips villous, the inner series 4-8 mm. long, glabrous on inner face, bearing a tuft of short, thick hairs on outer face, the outer series 1-3 mm. long, glabrous on inner surface, bearing a well defined tuft of short thick hairs on outer face. Ray flowers 15-35, the corolla tube 2-4 mm. long, the ligule 3-5 mm. long; disk flowers 35-40, the tube 2-3 mm. long, glabrous. Ray achenes 1.6-3.1 mm. long, trigonous, epappose, glabrous or slightly sericeous. Disk achenes 1.4-3.0 mm. long, obovate, compressed, densely sericeous. Pappus of two series, the inner series of numerous barbellate bristles, 3.8-5.5 mm. long, reddish brown to white, the outer series squamellate-setaceous or of short barbellate bristles 0.2-0.4 mm. long, white or occasionally reddish brown. Receptacle flat, white, alveolate, the partitions terminated by unequal chartaceous points.

5a. *H. subaxillaris* var. *subaxillaris*

Inula subaxillaris Lam., Encyc. Méth. Bot. 3: 259 col. 2. 1789.

Inula punctata Muhl., Cat. 76. 1813.

Inula scabra Pursh, Fl. Amer. Sept. 2: 531. 1814.

Heterotheca lamarckii Cass., Dict. Sci. Nat. 21: 131. 1821.

Chrysopsis scabra (Pursh) Ell., Sk. 2: 339. 1823.

Heterotheca scabra (Pursh) DC., Prod. 5: 317. 1836.

Stelmanis scabra (Pursh) Raf., Fl. Tellur. 2: 47. 1836.

Chrysopsis lamarckii (Cass.) Nutt. Trans. Am. Philos. Soc., Ser. II, 7: 315. 1841.

Heterotheca scabra, *alpha calycium* Torr. & Gray, Fl. N. Am. 2: 251. 1843.

Heterotheca scabra, *beta nuda* Torr. & Gray, Fl. N. Am. 2: 251. 1843.

Habit erect, leaves serrate, lateral veins prominent.

TIME OF FLOWERING: July to November, New Jersey to Georgia; throughout year along Gulf Coast.

TYPE AND TYPE LOCALITY: *D. Walter*, Carolina. Muséum National d'Histoire Naturelle, Paris (P). Photograph, Dr. G. H. M. Lawrence, Bailey Hortorium.

DISTRIBUTION AND HABITATS: Atlantic and Gulf Coasts from Delaware to northeastern Mexico. Sand dunes, beaches, fields and roadsides.

Shinners (1951) has dealt with the nomenclatural complexities of this species in some detail. For this reason this paper will deal quite briefly with the nomenclatural history.

Lamarck's (1789) description is somewhat vague and on its own would scarcely distinguish this species from several others in related genera. No indication is given as to where he acquired his specimen. The type specimen (P) bears only the notation "Walter, Carolina" and the reference to the Plukenet plate. This plate is not sufficiently detailed to make positive the identification of the species illustrated. Although unable to acquire the type on loan, I was able to make a positive identification of the type through the cooperation of Dr. Porterès of the Muséum National d'Histoire Naturelle and Dr. G. H. M. Lawrence, Bailey Hortorium, Ithaca, New York. Dr. Porterès sent portions of the type for study and compared material sent to him with the type, thus settling many questions. Dr. Lawrence kindly loaned me a photograph of the type which allowed a comparison of the habit of the type with specimens from herbaria in the United States. The results of this study showed that the type of *Inula subaxillaris* Lam. is a *Heterotheca* and is properly the type of the species now known as *Heterotheca subaxillaris* (Lam.) Britt. & Rusby. The suspicions of Cassini (1821) and De Candolle (1836) that the type of *Inula subaxillaris* was not a *Heterotheca* are thus shown to be baseless.

Inula punctata Muhl. (1813) referred to by Elliott and De Candolle as a synonym of *Inula scabra* Pursh is a *nomen nudum* and need not be considered for this reason, as well as for its lack of priority.

Inula scabra Pursh (1814) is illegitimate under Article 60 of the Rules of Nomenclature, since he cited *Inula subaxillaris* Lam. as a synonym. *Chrysopsis scabra* (Pursh) Ell. (1823), *Heterotheca scabra* (Pursh) DC. (1836) and *Stelmanis scabra* (Pursh) Raf. (1836) are all transfers of Pursh's illegitimate epithet and consequently are also illegitimate. De Candolle erroneously attributed the epithet to Nuttall (1818) in his transfer. Nuttall does not mark this species with an asterisk, as he did his own, and though there is no reference to Pursh under the species, he does comment in the introduction to Volume 1 (p. vii), "A brief Catalogue of the species is offered, which may be considered as supplementary to the recent and extensive Flora of North America by Frederick Pursh." It can be concluded therefore that Pursh is the author of the name.

In his description of *Heterotheca lamarckii*, Cassini (1821) cited *Inula subaxillaris* as a synonym and thus this name is also illegitimate according to Article 60. The binomial *Chrysopsis lamarckii*, created by Nuttall's (1818) transfer of this epithet, is also illegitimate.

The presence or absence of a crown on the ray achene is a character which not only occurs sporadically throughout most colonies, but one which may appear in either form in different heads of the same plant. The geographic distribution given by Torrey and Gray (1843) was not found in the large number of specimens examined in the course of this study. Under these conditions, both varieties *calycium* and *nudum* are considered ephemeral variants not worthy of formal recognition.

It is interesting to note that the transfer of the name of the type species to the genus *Heterotheca* as *H. subaxillaris* did not occur until seventy years after the description of the genus.

Representative specimens. **New Jersey:** Camden Co.: Camden, *Parker* (GH). **Pennsylvania:** Navy Yard, Philadelphia, *Canby* (F, NY). **Delaware:** New Castle Co.: *Wood* (US); Sussex Co.: *Williamson* (PH).

Virginia: Princess Anne Co.: Cape Henry, *Egler* 40-245 (NY).
North Carolina: Carteret Co.: Bogue, *Godfrey* 5836 (GH, US); New Hanover Co.: Carolina Beach, *Batchelder* (GH). **South Carolina:** Beaufort Co.: *Cuthbert* (NY); Charleston Co.: Isle of Palms, *Clausen & Trapido* 3574 (CU, NY, UC); Georgetown Co.: South Island, *Godfrey & Tryon* 1565 (CU, F, NY, UC, US). **Georgia:** Chatham Co.: *Githens* (PH); Decatur Co.: *Brinson, Thorne* 7636 (CU); Glynn Co.: Sea Island, *Cronquist* 5436 (NY, US). **Florida:** Alachua Co.: Gainesville, *Demaree* 10160 (CU); Brevard Co.: Rock Ledge, *Bart-ram* (PH); Collier Co.: Marco, *Deam* 60577 (SMU); Dade Co.: Buena Vista, *Moldenke* 5533 (NY); Duval Co.: Jacksonville, *Curtis* 1358 (CU, F, KANU, NEB, NY, P, PH, SMU, US); Franklin Co.: St. George Island, *Gauman* (NY, PH, UC); Gulf Co.: St. Vincent, *Tracy* 6359 (CU, NEB, NY, US); Hernando Co.: Brooksville, *Jones* 28 (CU, US); Hillsborough Co.: Davis Island, *Perkins* 860 (CU); Lake Co.: Eustis, *Nash* 1718 (CU, F, NEB, NY, P, PH, UC, US); Lee Co.: Fort Meyers, *Standley* 139 (F, NY, PH, US); Levy Co.: Cedar Keys, *Miller* 333 (US); Liberty Co.: 6 mi. E. Appalachicola, *Sargent* 6238 (SMU); Orange Co.: Lake Jovita, *O'Neill* (US); Palm Beach Co.: Gulfport, *Pilsbury* (CU); Putnam Co.: *Johnson and Barnhart* 2316 (NY); St. Johns Co.: Anastasia Island, *Perkins* 861 (CU); Volusia Co.: Tampa, *Degener* 5182 (NY). **Alabama:** Mobile Co.: *Mohr* (US). **Mississippi:** Hancock Co.: *Demaree* 29612 (TEX); Harrison Co.: *Bartram* (PH). **Louisiana:** Cameron Parish: *Correll* 9607 (NY). **Texas:** Cameron Co.: Del Mar, *Cory* (GH); Chambers Co.: *Tharp* 3191 (TEX, US); Galveston Co.: *Fisher* 654 (NY); Kleberg Co.: Padre Island, *Cory* 49139 (NY); Nueces Co.: Mustang Island, *War-nock* 21340A (TEX).

5b. *H. subaxillaris* var. *procumbens* var. nov.

Planta prostrata, foliorum laminis integris pauciserratisque, nervis lateralibus obscuris.

Habit procumbent, the leaves entire to remote-serrate, the lateral veins obscure.

TIME OF FLOWERING: Throughout the year.

TYPE AND TYPE LOCALITY: *R. M. Harper* 3801, on flattish dunes about a mile southwest of Dauphin Island Post Office, Mobile Co., Alabama, (GH). Isotypes (F, NY, PH, US).

DISTRIBUTION AND HABITATS: Eastern Florida to northeastern Mexico. Exposed beaches and drifting sand.

The type specimen was selected because it is typical of the variety and because it was distributed to a number of herbaria.

Representative specimens. **Florida:** Brevard Co.: Cape Canaveral, *Burgess* 683 (NY). **Alabama:** Mobile Co.: 1 mi. southwest of Dauphin Island Post Office, *Harper* 3801 (F, GH, NY, PH, US). **Mississippi:** Hancock Co.: Bay Saint Louis, *Munz* (CU); Harrison Co.: Mississippi City, *Lloyd & Tracy* 532 (NY); Jackson Co.: Horn Island, *Tracy* 4345 (NY). **Louisiana:** Cameron Parish: *Reed* 218 (US); Saint Bernard Parish:

Breton Island, *Tracy* (F, GH, US). **Texas:** Cameron Co.: Padre Island, *Johnston 54205* (TEX); Brazoria Co.: Freeport Beach, *Killip 43295* (TEX, US); Galveston Co.: Galveston Island, *Turner 1748* (SMU); Nueces Co.: Corpus Christi, *Tharp, Johnson and Weber 48-109* (TEX). **MEXICO:** Tamaulipas, south of Rio Grande, *Leseur 469* (US).

6. *H. psammophila* sp. nov.

Annua aromatica 0.5-2.0 m. alta. Caulis robustus ca. 8-12 mm. diametro striatus hispidulus vel pilosus. Folia plus minusve pilosa; infirma ovata, serrata, 4.5-7.0 cm. longa, 3.0-5.5 cm. lata, petiolis 1-2 cm. longis basin versus auriculatis; foliis caulinis lanceolatis integris vel serratis, 2-9 cm. longis, 0.5-3.0 cm. latis. Inflorescentia paniculato-corymbosa; capitula pedunculos nudos terminantia. Involucrum 0.8-1.2 cm. altum, 1.3-1.7 cm. latum, rotundato- vel lato-campanulatum. Phyllaria 4-6-seriata pilosa denseque glandulosa, exteriora 4-5 mm. longa, interiora 8-12 mm. longa. Flores radiati 20-30, corollae tuba 3-7 mm. longa, achaenia trigona 2.4-3.8 mm. longa epapposa glabra vel margine minute sericea. Flores discoidei 25-45, corollae tuba 5-9 mm. longa, achaenia obovata compressa 2.6-4.2 mm. longa dense sericea; pappis interioribus pilis, 6-9 mm. longis, barbellatis, dilute ferrugineis, exterioribus squamellatis, setaceis, vel nitis barbellatis dilutis ferrugineis. Receptaculum planum album denticulato-alveolatum.

Annual, aromatic herbs, 0.5-2 m. tall. Stem robust, 8-12 mm. in diameter, striate, hispid to pilose, the hairs up to 2.5 mm. in length. Leaves ovate to lanceolate, entire to serrate, sparsely pilose on upper and lower surfaces. Lower cauline leaves ovate, the lamina serrate, 4.5-7.0 cm. long, 2.0-5.5 cm. wide, petiolate, the petioles 1-3 cm. long, expanded into auriculate clasping bases. Middle and upper cauline leaves lanceolate, entire to serrate, 2-9 cm. long and 0.5-3 cm. wide, becoming cordate above. Inflorescence paniculate-corymbose, the heads terminal on leafless peduncles, the heads 1.3-1.7 cm. wide, 0.8-1.2 cm. high, hemispheric to broadly campanulate. Phyllaries in 4-6 series, the outer series 4-5 mm. long, the inner series 8-12 mm. long, pilose and densely glandular. Ray flowers 20-30, the corolla tubes 3-6 mm. long, the ligules 3-7 mm. long, the disk flowers 25-45, the tubes 5-9 mm. long, glabrous. Ray achenes 2.4-3.8 mm. long, trigonous, epappose, glabrous or more commonly sparsely sericeous on the angles. Disk achenes 2.6-4.2 mm. long, ovate, compressed, densely sericeous. Pappus of two series, the inner series of numerous barbellate bristles, 6-9 mm. long, tan; outer series squamellate-setaceous or of barbellate bristles 0.2-0.6 mm. long, tan. Receptacle flat, white, alveolate, the partitions terminated by unequal chartaceous points.

TIME OF FLOWERING: July to December.

TYPE AND TYPE LOCALITY: *B. L. Wagenknecht 4824*, sandy soil along edge of roadside ditch, 1 mi. s. Sedona, Yavapai Co., Arizona, August 23, 1957. (KANU).

(to be continued)